Insect movement and spatial dynamics determine trap crop effectiveness

Danish A. Ahmed[1, *], Noor Tahat[1], Isadora E. Fluck[2], Matthew H. Holden[3, 4], Joseph Bailey[5], Francisco Rubén Badenes-Pérez[6], Emma J. Hudgins[7], Philip E. Hulme[8], Fabrice Vinatier[9]

[1] Department of Mathematics and Natural Sciences, Gulf University for Science and Technology, Hawally, Kuwait

[2]University of Florida, Gainesville, Florida, USA

[3]School of Mathematics and Physics, The University of Queensland, St Lucia, Queensland, Australia

[4]Centre for Biodiversity and Conservation Science, The University of Queensland, St Lucia, Queensland, Australia

[5] School of Mathematics, Statistics and Actuarial Science, University of Essex, Colchester, UK

[6] Instituto de Ciencias Agrarias, Consejo Superior de Investigaciones Científicas, 28006 Madrid, Spain

[7] School of Agriculture, Food, and Ecosystem Sciences, The University of Melbourne, Parkville, Victoria, Australia

[8] The Centre for One Biosecurity Research, Analysis and Synthesis, Department of Pest Management and Conservation, Lincoln University, PO Box 85084, Canterbury, New Zealand

[9]LISAH, Univ. Montpellier, AgroParisTech, INRAE, Institut Agro, IRD, Montpellier, France

*Corresponding author (Ahmed.D@gust.edu.kw)

Abstract

Trap cropping diverts pest pressure away from cash crops, yet its effectiveness depends on pest movement behaviour and the retention or removal processes that occur after insects reach trap plants. We develop a one-dimensional movement-based modelling framework in which pest trajectories follow a biased correlated random walk within a spatially structured field containing trap-crop interception zones of varying size. The model represents attraction towards trap crops, directional persistence in pest movement, and post-encounter retention or removal within the trap crop zone. We analyse how movement behaviour, retention strength, and the allocation of land between cash and trap crops influence interception dynamics and

pest removal under ecologically realistic conditions. We find that trap crop effectiveness depends on the interaction between attraction and retention. Attraction alone does not guarantee pest suppression because insects may traverse the trap crop with residence times too short for removal processes to reduce pest abundance. In contrast, interception and retention mechanisms lead to suppression through distinct processes: strong entry interception leads to rapid pest removal, whereas behavioural arrestment increases trap crop occupancy and reduces emigration from the field. When retention is weak, insects escape after crossing the trap crop strip, limiting trap cropping effectiveness. The model reveals trade-offs among trap crop size, pest suppression, and the allocation of land between trap and cash crops. By linking pest movement dynamics with trap crop spatial allocation, this framework provides a mechanistic basis for predicting trap cropping performance and highlights the importance of retention in improving trap-based pest management strategies.

Keywords Trap cropping, integrated pest management, insect movement, biased correlated random walk, directional persistence, behavioural arrestment, pest retention

1. Introduction

Pest control remains a central challenge in agriculture, and chemical pesticides have long been the dominant management tool. However, long-term reliance on pesticides has produced a range of well-documented problems, including the evolution of pest resistance, impacts on non-target organisms, risks to human health, and widespread environmental contamination (Sparks and Nauen, 2015; Savary et al., 2019; De Souza et al., 2020; Tooker and Pearsons, 2021). These concerns have motivated increasing interest in pest management strategies that reduce chemical inputs while maintaining crop productivity and economic viability (Gurr et al., 2003; Cook et al., 2007; González-Chang et al., 2019; Angon et al., 2023). Many strategies leverage biotic interactions—whether between a pest and its natural enemies (e.g., insect–parasitoid relationships), among individuals of the same species (e.g., pheromone-based trapping), or between the pest and its host plant. For the latter, trap cropping has emerged as a promising strategy within integrated pest management. In this strategy, the trap crop is planted alongside the crop grown for harvest or profit (i.e., the cash crop) in order to divert pest pressure away from the cash crop (Hokkanen, 1991; Shelton and Badenes-Pérez, 2006). By exploiting natural behavioural cues rather than relying solely on chemical control, trap cropping offers a potentially sustainable means of reducing pest damage as part of a

broader pest management programme and has been applied in a variety of agricultural systems (Shelton and Badenes-Pérez, 2006; Lu et al., 2009; Tillman and Cottrell, 2012).

Trap cropping success depends on several interacting ecological processes rather than attraction alone (Shelton and Badenes-Pérez, 2006). For a trap crop to function effectively, pests must first encounter the trap crop plants and then remain there long enough for mortality processes to occur or for movement to the cash crop to be prevented (Hokkanen, 1991; Hilje et al., 2001; Badenes-Pérez et al., 2005b, 2005a; Shelton and Badenes-Pérez, 2006; Badenes-Pérez, 2025). Empirical and theoretical studies therefore emphasise three key determinants of trap crop performance: pest attraction to the trap plant, pest movement and spatial redistribution within the field, and the retention or mortality of insects after they reach the trap crop (Cook et al., 2007; Holden et al., 2012). Modelling approaches have shown that pest movement behaviour and spatial configuration strongly influence how rapidly insects encounter trap crops and how pest populations redistribute between crop patches (Perry and Wall, 1984; Banks and Ekbom, 1999). At the same time, both empirical observations and theoretical models indicate that high retention within the trap crop is often necessary for effective pest suppression, because pests that disperse away from the trap crop can quickly recolonise the cash crop (Shelton and Nault, 2004; Cook et al., 2007; Holden et al., 2012). Consequently, successful trap cropping systems frequently rely on additional processes that increase pest mortality or prevent escape, such as natural enemies, targeted pesticide applications, or host plants on which pests have reduced survival (Shelton and Badenes-Pérez, 2006; Badenes-Pérez et al., 2017; Badenes-Pérez, 2025). These interacting mechanisms make it difficult to disentangle the relative contributions of attraction, movement behaviour, and retention in field experiments. Distinguishing these processes is necessary both for understanding trap crop performance and for guiding practical management decisions under specific crop and host traits.

Mathematical and simulation-based models have become valuable tools for exploring trap cropping dynamics (Perry and Wall, 1984; Hannunen, 2005; Holden et al., 2012; Fenoglio et al., 2017). Modelling therefore provides a complementary perspective by allowing these processes to be examined individually under controlled assumptions (Zurell et al., 2010). For example, the spatial arrangement of trap crops can interact strongly with pest mobility in determining interception dynamics (Banks and Ekbom, 1999). Existing modelling frameworks include diffusion-based movement (Perry and Wall, 1984; Hannunen, 2005), spatially explicit individual-based frameworks (Vinatier et al., 2012; Garcia et al., 2021), and

patch-based models incorporating biological control processes (Banks and Laubmeier, 2024). Trap crop effectiveness appears to depend on the combined effects of attraction, retention, and plant distribution rather than on any single factor (Holden et al., 2012). Understanding the relative importance of each of these factors in a particular local context is crucial for designing an optimal trap crop array under constraints on land allocation and crop production (Holden, 2026b).

A central component of trap crop effectiveness is how pests move through agricultural landscapes. Individual movement is often modelled using random walk frameworks that describe trajectories as sequences of steps and turning angles (Codling et al., 2008). While simple random walk models lead to diffusive motion at large spatial and temporal scales (Kareiva, 1983; Petrovskii et al., 2012), many insects exhibit directional persistence, maintaining their heading over successive steps. This behaviour is captured by correlated random walk models, which have been used to represent the movement of many arthropods (Kareiva and Shigesada, 1983; Byers, 2001; Reynolds et al., 2013; Petrovskii et al., 2014; Ellis et al., 2020; Ahmed et al., 2023). When directional responses to environmental cues, such as host-plant volatiles or visual signals, are also incorporated, the model becomes a biased correlated random walk, allowing individuals to combine directional persistence with attraction towards environmental stimuli (Codling et al., 2010, 2008). Despite the extensive use of biased correlated random walk models in movement ecology (Turchin, 1998; Barton et al., 2009; Bailey et al., 2018; Alqubori and Petrovskii, 2022), they have not previously been applied to trap cropping. Current trap cropping models typically simplify pest movement and therefore do not jointly represent directional persistence, attraction towards trap crops, and retention after arrival (Garcia et al., 2021; Banks and Laubmeier, 2024; Holden, 2026a). As a result, the combined effects of movement trajectories incorporating directional persistence, spatially varying attraction, and behavioural retention remain unexplored within a single mechanistic framework, leaving an important gap in our understanding of the effectiveness of trap cropping.

To address this gap, we develop a flexible movement-based modelling framework in which pest trajectories follow a biased correlated random walk within an agricultural field containing a trap crop interception zone and allowing temporary emigration. The model represents three key processes governing trap-cropping performance: attraction towards the trap crop, directional persistence in pest trajectories, and retention or removal of insects after arrival in the trap zone (Hokkanen, 1991). Within the cash crop, insects move under

directional persistence combined with attraction towards trap crop-associated cues, while within the trap crop, movement becomes locally diffusive, representing milling (i.e., local wandering) or browsing (i.e., local exploratory movement) behaviour following arrival. Post-arrival removal is incorporated through mechanisms operating either upon entry into the trap crop or during residence within it, capturing management efforts such as targeted control measures and ecological processes such as enhanced predation. Reduced movement within the trap crop represents behavioural retention and restricted escape after arrival, including effects analogous to physical barriers or landscape features that limit pest movement (Hilje et al., 2001). Because these mechanisms are represented explicitly and can vary independently, the framework can reproduce a range of trap cropping scenarios observed in agricultural systems. For clarity and tractability, the model is formulated in one spatial dimension, representing cross-sections through common trap cropping configurations, such as border plantings, perimeter strips, or field margins, while allowing the behavioural mechanisms governing pest interception to be examined separately (Perry and Wall, 1984; Banks and Ekbom, 1999).

Using this framework, we investigate how behavioural and spatial processes jointly determine trap crop effectiveness. Specifically, we examine (i) how differences in movement behaviour affect the rate at which pests encounter and enter the trap crop zone, (ii) how retention strength and trap crop size interact to determine cumulative pest removal and protection of the cash crop, and (iii) how allocating land between trap crops and productive cash crops influences overall agricultural benefit. These analyses provide a mechanistic basis for the design of trap cropping systems as effective, low-input pest management strategies within integrated pest management programmes.

2. Methods

2.1 Model formulation

We model the movement of a population of N insect pests within a one-dimensional agricultural field of total length L, partitioned into two contiguous crop zones. The cash crop occupies $(0, kL)$, while the terminal trap crop strip occupies (kL, L), where k (with $0 < k < 1$) represents the proportion of the field allocated to the cash crop (Fig. 1). Individuals move throughout the domain and may repeatedly enter and leave the trap crop region, undergoing behavioural modification and removal within the trap. The one-dimensional representation reflects movement along a field transect terminating in a trap crop strip, which is the primary

determinant of encounter and interception in border trap-cropping systems. The spatial domain length L represents the effective scale over which insects redistribute within a field and encounter trap crops. Field margins and perimeter plantings in row-crop systems typically operate over distances of tens to a few hundred metres. The proportion of the domain occupied by the cash crop, k, therefore lies between approximately 0.70 and 0.90, corresponding to trap crop designs in which roughly 10–30% of the field edge is devoted to interception rather than production, although modelling studies suggest that efficient interception may often be achieved with trap crop fractions of approximately 5–20% (Holden, 2026b).

To capture both directional persistence and attraction to trap crops, movement within the cash crop is modelled as a biased correlated random walk representing primarily local movement of arthropod pests during host searching and crop exploitation, such as the Colorado potato beetle, *Leptinotarsa decemlineata*, for which movement behaviour, host-oriented responses, and trap-crop interception have been extensively studied (Hunt and Whitfield, 1996; Landolt et al., 1999; Martel et al., 2005; Gui et al., 2012; Boiteau et al., 2014). The field occupies the interval $(0, L)$, but individuals may temporarily emigrate beyond either boundary, into the regions $x < 0$ or $x > L$, while remaining active and able to return; crossing a field boundary therefore does not itself remove individuals from the population (Potting et al., 2005). Movement is implemented in discrete steps. The variable Δt serves only as a time scaling unit; movement dynamics are step-based and do not depend explicitly on Δt. Each insect individual i is characterised by its position $x_i(t)$ at step t, which evolves according to Eq. (1):

$$x_i(t) = x_i(t-1) + \delta_i(t)\, s_i(t), \tag{1}$$

where $\delta_i(t)$ is either −1 or +1, denoting leftward or rightward movement, respectively (Fig. 1), and $s_i(t) > 0$ is the step length (Turchin, 1998; Okubo and Levin, 2001). Ecologically, this formulation represents a sequence of movement decisions in which insects continue local foraging within the cash crop, move parallel to the trap crop, or advance towards the trap crop strip.

Step lengths $s_i(t)$ are drawn independently from a half-normal distribution, with probability density function (Eq. (2)),

$$f(\mathrm{s}) = \frac{\sqrt{2}}{\sigma\sqrt{\pi}} \exp\left(-\frac{s^2}{2\sigma^2}\right), \qquad s > 0, \tag{2}$$

and scale parameter $\sigma > 0$ (Ahmed et al., 2025). The mean $E[s]$ and variance $V[s]$ of this distribution are given by Eq. (3):

$$E[s] = \sigma\sqrt{\frac{2}{\pi}}, \qquad V[s] = \sigma^2\left(1 - \frac{2}{\pi}\right). \tag{3}$$

This distribution reflects the tendency of insects to make frequent short exploratory movements interspersed with occasional longer displacements.

Parameter values correspond to spatial and behavioural scales commonly observed for mobile insect pests in agricultural landscapes where trap crops are deployed. Movement distances are governed by the step-length scale σ, which represents local motility rather than maximum dispersal capacity. Trap-cropping systems have been developed for mobile pests such as Colorado potato beetle, *Leptinotarsa decemlineata*, in solanaceous crops (Caprio and Grafius, 2017) and striped cucumber beetle, *Acalymma vittatum*, in cucurbit systems (Cavanagh et al., 2009). In this context, metre-scale movement steps provide a plausible representation of local exploratory movement within crop rows, between neighbouring plants, and near crop interfaces. The half-normal step-length distribution therefore produces frequent short exploratory movements while allowing occasional longer displacements that facilitate encounters with trap crop boundaries. Empirical studies have shown that movement-distance features of beetles, such as step length and displacement, can vary according to local conditions, including vegetation cover, physical resistance, feeding or foraging state, and temperature (Wiens et al., 1997; Jopp, 2006; Gui et al., 2012; Gireesh and Joseph, 2022), supporting the interpretation of σ as a flexible measure of pest motility. A summary of all model parameters, definitions, and ecological interpretations is provided in Table S1 of the Supplementary Information.

2.2 Directional persistence and bias

Movement direction $\delta_i(t)$ for individual *i* at time *t* is determined by either directional persistence, i.e., the tendency to maintain the recent heading, or environmental bias. At $t = 0$, initial directions are assigned independently at random, with $\delta_i(0) = +1$ or $\delta_i(0) = -1$ with equal probability. In the cash crop, the direction $\delta_i(t)$ is governed by directional persistence, $\delta_i^{\text{pers}}(t)$, with probability $(1 - \omega)$, and by attraction bias, $\delta_i^{\text{bias}}(t)$, with complementary probability ω; as defined in Eq. (4):

$$\delta_i(t) = \begin{cases} \delta_i^{\text{bias}}(t), & \text{with probability } \omega, \\ \delta_i^{\text{pers}}(t), & \text{with probability } 1 - \omega, \end{cases} \tag{4}$$

thus the environmental bias weight ω lies in [0, 1] and controls how frequently insects respond to environmental cues (i.e., trap crop attractiveness) relative to persistence-driven movement (Fig. 1).

Persistence is defined relative to the previous direction $\delta_i(t-1)$ according to Eq. (5):

$$\delta_i^{\text{pers}}(t) = \begin{cases} -\delta_i(t-1), \text{ with probability } \frac{1-\alpha}{2}, \\ \delta_i(t-1), \text{ with probability } \frac{1+\alpha}{2}, \end{cases} \quad (5)$$

where $\alpha \in [-1, 1]$ controls the strength of directional memory between successive movement steps.

Bias at time t is defined as attraction towards (+1) or aversion away (−1) from the trap crop, and is implemented according to Eq. (6):

$$\delta_i^{\text{bias}}(t) = \begin{cases} -1, \text{ with probability } \frac{1-\beta(x_i(t-1))}{2}, \\ +1, \text{ with probability } \frac{1+\beta(x_i(t-1))}{2}, \end{cases} \quad (6)$$

where $\beta(x_i)$ is the strength of bias as a function of insect i's position relative to the cash-trap boundary. Specifically, for x_i in $(0, kL)$,

$$\beta(x) = \beta_{\max} \left(\frac{x}{kL}\right)^{\nu}, \quad (7)$$

where $\beta_{\max} \in [0, 1]$ is the maximum attraction strength at the cash–trap crop interface $x = kL$, and therefore $\beta(x) \in [0, \beta_{\max}]$ on $(0, kL)$. The parameter $\nu \geq 0$ controls how attraction varies with distance from the trap crop. When $\nu = 0$, insects are equally attracted to the trap crop regardless of their position in the cash crop, producing a uniform bias. For $\nu > 0$, attraction becomes increasingly dependent on proximity to the trap crop, so insects become more likely to move towards the trap crop as they get closer to it. When $\nu = 1$, attraction increases linearly with proximity (Fig. 1). Values of ν between 0 and 1 produce a broader zone of attraction that extends farther into the cash crop, whereas $\nu > 1$ concentrates the effect of attraction near the cash-trap crop boundary. Ecologically, lower values of ν represent trap-crop cues that can influence insect movement over larger spatial scales, whereas higher values represent cues whose effects are strongest when insects are already close to the trap crop. In the model, cue-driven bias is switched off outside the cash crop, so we set $\beta(x) = 0$ in the trap crop (kL, L)

and in both emigration zones ($x < 0$ and $x > L$), reflecting neutral movement outside the cash crop.

Operationally, when individuals are in the cash crop, the model selects at each time-step a direction defined by either persistence, $\delta_i^{pers}(t)$, or bias, $\delta_i^{bias}(t)$, according to the parameter ω, representing the balance between persistence-driven movement and behavioural responses to environmental cues associated with the trap crop. Outside the cash crop i.e., within the trap crop strip (kL, L) and in the emigration zones $x < 0$ and $x > L$, directions are not updated using persistence or bias. Instead, movement follows an unbiased one-dimensional random walk (a simple random walk), with $\delta_i(t) = +1$ or $\delta_i(t) = -1$ with equal probability at each step. In this way, the model distinguishes between directional, cue-responsive movement in the cash crop and non-directional movement after insects enter the trap crop, reflecting the retention phase in which individuals tend to remain within a preferred host patch once they have found it.

In particular, an individual's foraging state may influence both directional persistence and attraction. "Hungry" beetles have been shown to move with greater displacement and straighter paths than satiated individuals, suggesting that feeding status can increase persistence in movement trajectories (Gui et al., 2012). In our approach, directional persistence values within the range $\alpha \approx 0–0.5$ correspond to weak-to-moderate directional memory and produce movement paths that are neither purely diffusive nor strongly ballistic. Such intermediate persistence is commonly reported in insect foraging trajectories, where individuals maintain their heading over short intervals but frequently reorient in response to local cues (Rusman et al., 2024; Chaianunporn and Hovestadt, 2025). Attraction can likewise shape movement through biologically meaningful cues, including volatiles released by damaged plants and male-produced aggregation pheromones, which may bias movement toward the trap crop rather than resulting in random redistribution across the field (Landolt et al., 1999; Brzozowski et al., 2020). In the model, this is represented through moderate bias strengths ($\beta_{max} \approx 0.1–0.5$), consistent with intermittent orientation toward cues rather than deterministic movement toward the trap crop.

2.3 Arrestment

On arrival at a host plant, insects often reduce locomotion, increase turning behaviour and settle. This arrestment behaviour is incorporated to represent reduced mobility and increased residence time within the trap crop region. In the present model, arrestment is represented as

a reduction in movement scale rather than as a discrete stationary state. Individuals located within the trap crop, defined by the interval (kL, L), move with unbiased reorientation and a reduced step-length scale, given by $\sigma_{trap} = \rho\sigma_{cash}$, where $0 < \rho < 1$. This reduction captures the tendency of individuals encountering the trap crop to slow down and remain locally confined while still permitting small-scale movements within or among neighbouring plants (Fig. 1).

The reduction in movement associated with the trap crop is restricted to this region and does not apply elsewhere in the domain. Individuals within the cash crop move with the full step-length scale σ_{cash}, although the underlying step-length distribution still permits occasional short movements. These short movements arise from the stochastic movement process rather than from a habitat-specific reduction in mobility. Individuals that temporarily emigrate beyond either field boundary ($x < 0$ or $x > L$) also move without arrestment, retaining the cash crop step-length scale and undergoing unbiased reorientation.

This reduction in displacement may contribute to local aggregation on particular plants in response to local conditions and changes in behavioural state (e.g., the post-diapause state in beetles; Caprio and Grafius, 2017). Values of $\rho \ll 1$ correspond to reduced mobility and increased residence within the trap crop, allowing retention to be modelled as an ecologically relevant response of the pest to crop management. Thus, arrestment is used here in the broader sense of effective local confinement rather than complete cessation of movement.

2.4 Emigration

At both field boundaries, $x = 0$ and $x = L$, individuals may move outside the domain into the regions $x < 0$ or $x > L$, respectively. They are then classified as emigrated but remain active and may subsequently re-enter the field. While outside the domain, individuals move with unbiased reorientation, without arrestment, and with the full cash-crop step-length scale. Thus, boundary crossing represents temporary emigration rather than permanent loss from the population. This open-boundary formulation allows population dynamics to be partitioned into cash crop occupancy, trap crop occupancy, removal, and reversible emigration beyond either field boundary (Fig. 1).

2.5 Within-trap crop removal and residence time

Individuals entering the trap crop region are subject to two distinct removal mechanisms: (*i*) an entry-triggered removal applied immediately upon crossing from the cash crop into the

trap crop, and (*ii*) a continuous within-trap crop removal process acting while individuals remain inside the trap crop (Rhino et al., 2016; Han et al., 2024; Badenes-Pérez, 2025). These mechanisms represent different ecological and management processes and operate on different temporal scales.

The entry-triggered removal is governed by a probability γ_{entry}, which is applied at the moment an individual enters the trap crop from the cash crop (Fig. 1). This term captures rapid interception processes occurring at the crop interface, such as immediate contact with insecticide-treated borders or sticky trap plants, physical trapping, or edge-focused predation (Holden et al., 2012). An individual crossing into the trap crop is removed with probability γ_{entry}; if not removed, it continues to move within the trap crop and becomes subject to within-trap crop processes thereafter. Importantly, γ_{entry} is independent of the simulation time step and does not accumulate with time spent in the trap crop. If an individual subsequently exits the trap crop into the cash crop and later re-enters, the entry-triggered removal probability γ_{entry} is applied again upon each re-entry, while within-trap crop removal operates only during periods in which the individual is located inside the trap crop.

Individuals that survive entry are subsequently exposed to within-trap crop removal, which is parameterised in terms of a daily probability of removal, denoted γ_{day} (Fig. 1). This represents the probability that an individual is removed over a full day conditional on remaining within the trap crop for that entire day. Ecologically, this may represent processes acting during residence in the trap crop, including prolonged insecticide exposure, physiological stress, or pressure from predators and parasitoids concentrated within the trap crop patch (Badenes-Pérez et al., 2006; Macfadyen and Muller, 2013; Salat-Moltó et al., 2023; Badenes-Pérez, 2025). In the model, γ_{day} is the primary parameter controlling the strength of within-trap crop removal. Model simulations are performed using a discrete time step of length Δt (hours). To ensure consistency across time scales, γ_{day} is converted into an equivalent per-step removal probability $\gamma_{\Delta t}$ according to Eq. (8):

$$\gamma_{\Delta t} = 1 - (1 - \gamma_{\text{day}})^{\Delta t/24}. \quad (8)$$

This formulation ensures that survival probabilities compound correctly across time steps, such that an individual that remains continuously within the trap crop for 24 hours experiences an overall removal probability of exactly γ_{day}. Within the simulation, removal due to within-trap crop processes is implemented by drawing a Bernoulli trial with probability $\gamma_{\Delta t}$ at each movement step for individuals located in the trap crop.

The corresponding expected time to removal during continuous residence in the trap crop can be interpreted directly from γ_{day}. Under the assumption of continuous exposure within the trap crop, the expected time to removal is approximately (Eq. (9)):

$$E(T_{\mathrm{trap}}) \approx \frac{1}{\lambda} \text{ days}, \quad (9)$$

where the daily hazard rate is given by Eq. (10):

$$\lambda = -ln(1 - \gamma_{\mathrm{day}}) \text{ day}^{-1}. \quad (10)$$

For small γ_{day}, this reduces to $E[T_{trap}] \approx 1 / \gamma_{day}$. For instance, $\gamma_{day} = 0.2$ corresponds to an expected time to within-trap removal of approximately five days for individuals that remain continuously within the trap crop.

In practice, realised residence times may be shorter than this expectation due to removal upon entry or movement-mediated exits from the trap crop. Accordingly, γ_{day} should be interpreted as a conditional daily hazard of removal, rather than a fixed trapping duration. Together, γ_{entry} and γ_{day} allow the model to distinguish between rapid edge-driven interception and slower, time-dependent removal within the trap crop, while remaining robust to changes in time step size and movement dynamics.

Both removal processes may also be influenced by the intensity and spatial distribution of natural-enemy pressure. Entry-triggered removal and within-trap removal may be greater in trap crop patches or along boundaries where predators and parasitoids concentrate (Macfadyen and Muller, 2013; Salat-Moltó et al., 2023). Natural enemies concentrated along the cash crop–trap crop boundary may contribute to entry-triggered removal, whereas those active within the trap crop may contribute to continued removal during residence. Simulation durations of several weeks correspond to typical deployment periods of trap crops within a growing season, allowing individual-scale movement decisions to accumulate into field-scale redistribution and interception dynamics.

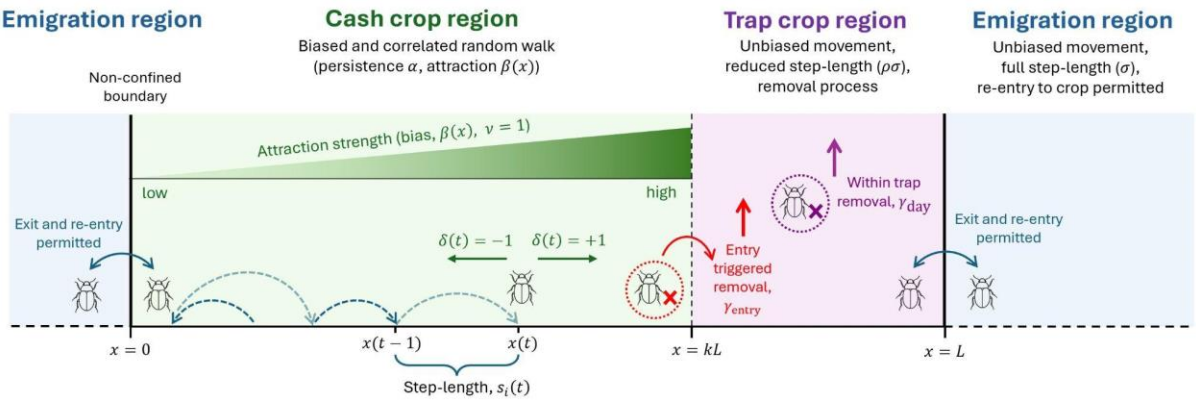

Figure 1 Conceptual schematic of the movement-based trap-cropping model. The one-dimensional landscape is partitioned into four regions: a left-hand emigration region ($x < 0$), a cash crop region occupying $(0, kL)$, a terminal trap crop strip occupying (kL, L), and a right-hand emigration region ($x > L$). Within the cash crop, insects move according to a biased correlated random walk, where movement is determined by the combined effects of directional persistence (α) and attraction towards the trap crop (β(x)). Attraction strength increases towards the cash crop–trap crop interface, reflecting host-associated cues that bias movement towards the trap crop. For illustrative purposes, the case of a linear attraction bias (ν = 1) is shown. Movement occurs in discrete steps of length $s_i(t)$, with direction $\delta_i(t) = \pm 1$ indicating leftward or rightward movement. The step lengths shown are schematic and are not drawn to scale relative to the field length. Upon entering the trap crop region, directional bias and persistence are removed and movement becomes unbiased. Insects may exhibit arrestment, represented by a reduction in step length by a factor ρ, resulting in increased residence time within the trap crop. Two removal mechanisms operate within the trap crop. Entry-triggered removal occurs immediately upon crossing from the cash crop into the trap crop with probability γ_{entry}, representing rapid interception processes such as insecticide-treated borders, physical trapping, or edge-focused predation. Individuals that remain in the trap crop are subsequently exposed to within-trap removal at a daily probability γ_{day}, representing mortality or suppression occurring during residence within the trap crop. Individuals crossing either field boundary, $x = 0$ or $x = L$, enter an emigration region where movement is unbiased and occurs at the full cash-crop step-length scale. Emigrated individuals are not removed from the system and may subsequently re-enter the field. The framework therefore explicitly separates four key processes governing trap crop performance: attraction towards the trap crop, directional persistence during movement, behavioural retention within the trap crop, and pest removal following trap crop encounter. These processes jointly determine pest redistribution among the cash crop, trap crop, removed, and emigrated population states.

2.6 Simulating trap cropping

Figure 2 illustrates the spatio-temporal dynamics generated by the movement-based trap cropping model under uniform initial conditions. At the outset, pests are evenly distributed across the cash crop region $(0, kL)$ with $k = 0.8$. This provides a baseline scenario without imposing localised emergence or edge-biased colonisation. As individuals move under directional persistence and probabilistic attraction towards the trap crop strip, the spatial distribution becomes progressively shaped by redistribution within the cash crop, movement across the field boundaries, and selective loss near the cash crop–trap crop interface. Upon

crossing from the cash crop into the trap crop, individuals are immediately removed through entry-triggered interception with probability ($\gamma_{entry} = 0.1$). Individuals that are not removed upon entry continue to move within the trap crop strip under arrestment, characterised by reduced step lengths ($\rho = 0.1$) and unbiased reorientation, which increases residence time within the trap crop. While remaining in the trap crop, individuals are subject to removal governed by a daily removal probability ($\gamma_{day} = 0.2$), leading to cumulative losses among individuals that remain within the trap crop. At the field scale, individuals that move beyond either boundary, into the regions $x < 0$ or $x > L$, are classified as emigrated but remain active and may subsequently re-enter the field, moving without arrestment and with the same step-length scale as in the cash crop. As movement, removal, and reversible emigration act repeatedly, the dynamics are governed primarily by access to the trap boundary, retention within the trap crop, and movement across the field boundaries, rather than by any initial spatial structure.

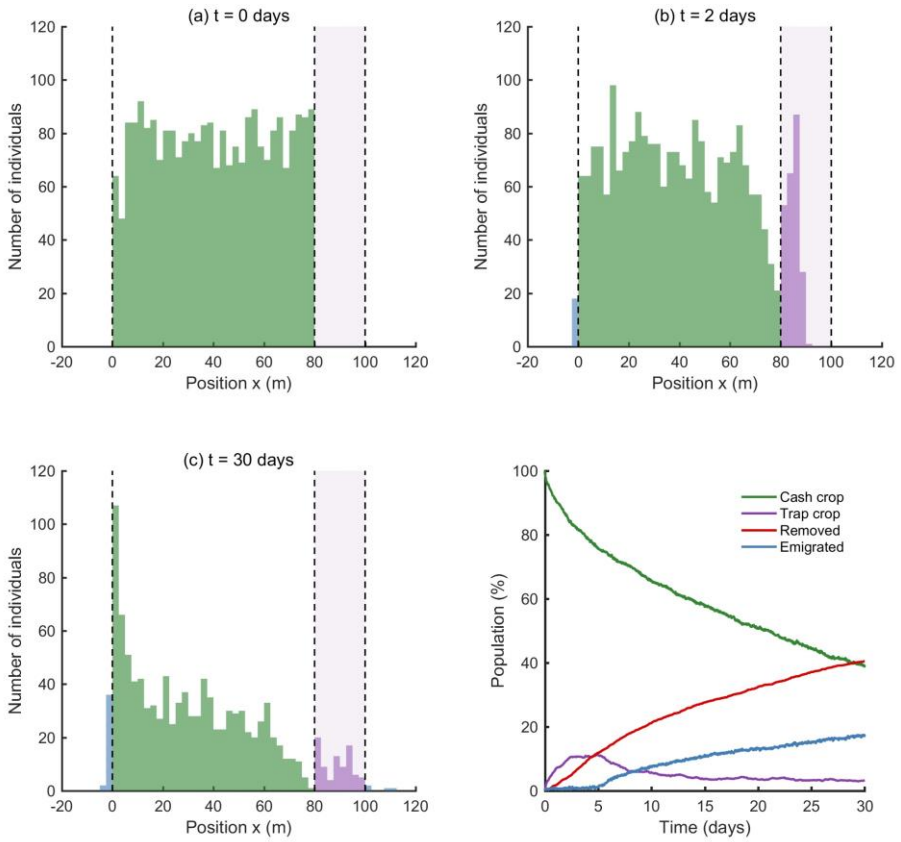

Figure 2 Trap cropping dynamics in one-dimensional space simulated using a biased correlated random walk with arrestment, probabilistic removal, and emigration. (a–c) Histograms with 2.5 m spatial bins show insect positions at $t = 0$, 2, and 30 days within a field of length $L = 100$ m. The cash crop occupies the interval $(0, kL)$ and the trap crop occupies the terminal strip (kL, L), with $k = 0.8$ (vertical dashed line at $x = 80$ m). Individuals are initially distributed uniformly within the cash crop

region, with total population size N_0 = 2,500. Movement occurs in discrete steps of duration Δt = 0.5 h, with step lengths drawn from a half-normal distribution (σ_{cash} = 1 m; Eq. 2). Within the cash crop, movement combines directional persistence (α = 0.2) with probabilistic environmental bias toward the trap crop, applied with probability ω = 0.5 and increasing linearly with distance from the cash crop–trap crop interface (β = 0.1, ν = 1). Inside the trap crop, environmental bias is suppressed and movement becomes unbiased with reduced step scale $\sigma_{trap} = \rho\sigma_{cash}$, with ρ = 0.1, representing arrestment behaviour. Individuals may be removed via two mechanisms: entry-triggered removal upon crossing from the cash crop into the trap crop, with probability γ_{entry} = 0.1, and removal while remaining within the trap crop, specified by a daily removal probability (γ_{day} = 0.2). Individuals that move beyond either field boundary, into the left-hand emigration zone ($x < 0$) or beyond the right-hand boundary ($x > L$), are classified as emigrated but remain active and may subsequently re-enter the field; while outside the domain, movement is unbiased and occurs with the same step-length scale as in the cash crop (σ_{cash}). (d) Temporal partitioning of the population into four mutually exclusive classes: individuals remaining in the cash crop, individuals remaining in the trap crop, individuals removed within the trap crop, and individuals currently located outside either field boundary but may subsequently re-enter the domain. All curves are expressed as a percentage of the initial population size N_0 and together account for the entire population at each time point.

3. Results

3.1 Movement dynamics

The spatial structure of the attraction field influenced population outcomes (Fig. 3). Uniform attraction profiles (ν = 0) produced greater depletion of the cash crop (Fig. 3a) and higher cumulative removal (Fig. 3c) than profiles concentrated near the trap crop boundary (ν = 2). This indicates that attraction cues acting across the crop interior recruit insects towards the trap crop more effectively than signals concentrated near the cash crop–trap crop boundary. Trap crop area also affected the balance between removal and emigration. Larger trap crop size (k = 0.7) generated higher removal (Fig. 3c), whereas smaller trap crop size (k = 0.9) was associated with greater emigration beyond either field boundary (Fig. 3d). Thus, smaller trap crop strips were associated with a greater proportion of individuals outside the field and lower cumulative removal. Trap crop occupancy remained low across all scenarios (Fig. 3b) and generally peaked at intermediate values of β_{max}. Even under strong attraction, the trap crop did not accumulate large resident populations, consistent with its role as a transient retention and removal zone rather than a refuge.

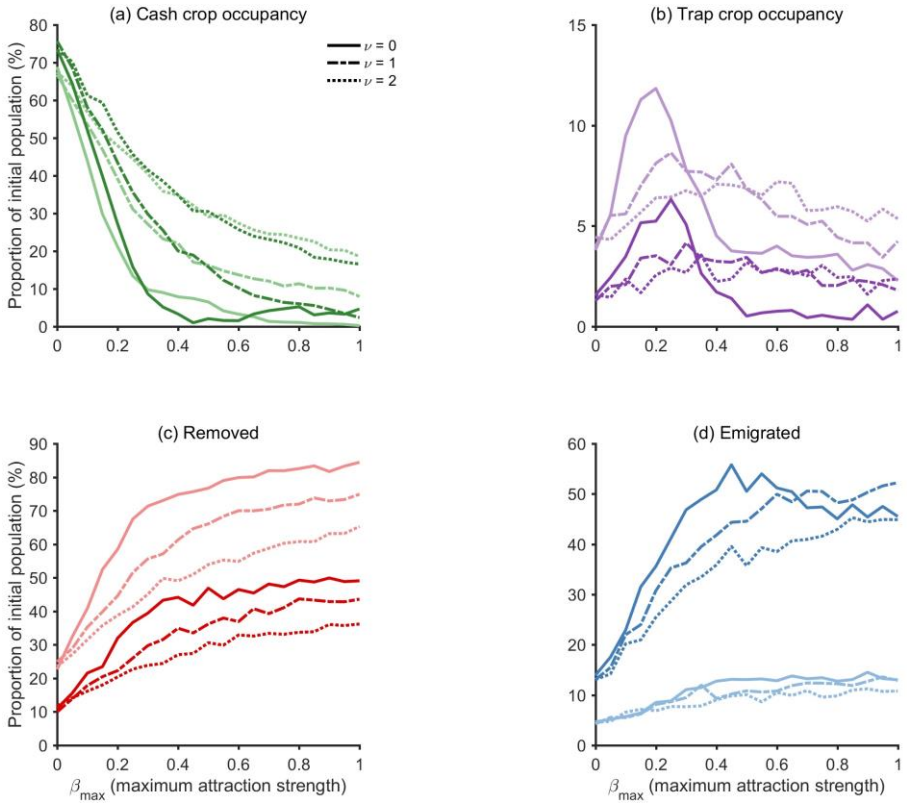

Figure 3 Population partitioning at t = 15 days as a function of maximum attraction strength β_{max}, varied from 0 to 1, for different spatial bias profiles ν and cash crop fractions k. Panels show the proportions of the population (a) remaining in the cash crop, (b) occupying the trap crop, (c) cumulatively removed, and (d) currently emigrated beyond either field boundary. Results are shown for k = 0.7 (30% trap crop; lighter shade) and k = 0.9 (10% trap crop; darker shade), in each panel. All other parameters are as in Fig. 2.

Cash-crop occupancy was shaped by interactions among directional persistence (α), environmental bias weight (ω), and maximum attraction strength (β_{max}) (Fig. 4). When β_{max} = 0, differences among ω values were relatively small and showed no consistent ordering, whereas occupancy generally declined as α became strongly positive. Increasing β_{max} produced greater separation among the ω curves. At β_{max} = 0.25 and 0.5, larger bias weights generally resulted in lower cash-crop occupancy across most of the persistence range, indicating that more frequent responses to the attraction cue promoted movement out of the cash crop. By contrast, when ω = 0, occupancy remained similar across attraction strengths because the cue did not influence direction selection. The effect of α also depended on ω: occupancy declined markedly at high positive persistence when environmental bias was weak, whereas stronger bias reduced sensitivity to α over much of the intermediate range. Near α = 1, occupancy fell sharply and the curves tended to converge, particularly at higher attraction strengths.

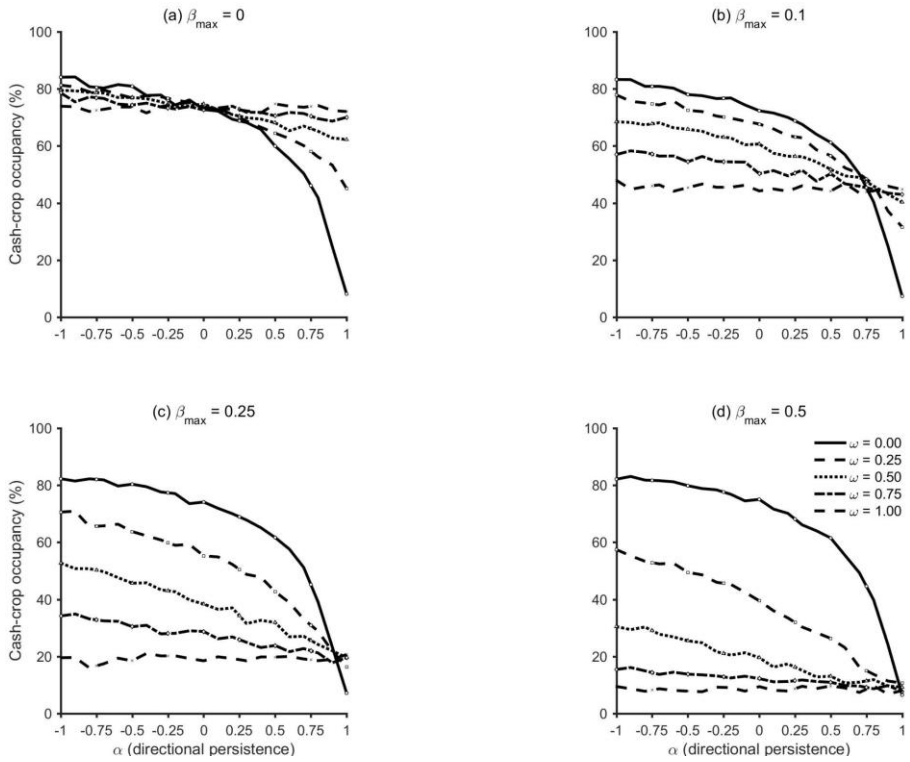

Figure 4. Cash crop occupancy across directional persistence (α) for different bias weights (ω) and attraction strengths (β_{max}). Each panel shows the proportion of N_0 = 2,500 insects remaining in the cash crop after 15 days as α varies from −1 to 1, for five environmental bias weights (ω = 0, 0.25, 0.5, 0.75, 1) at a specified maximum attraction strength β_{max} = 0, 0.1, 0.25, or 0.5. All other parameters are as in Fig. 2.

When attraction was absent (β_{max} = 0), cash crop occupancy remained relatively high across most of the parameter space but declined sharply under strongly positive directional persistence (α ≈ 1), particularly when the environmental bias weight was low (ω ≈ 0; Fig. 5). In this case, increasing ω weakened the influence of persistence by replacing persistence-driven updates with unbiased directional choices. As attraction strength increased, the region of low cash crop occupancy expanded across the (α, ω) parameter space. At β_{max} = 0.1 and 0.25, occupancy declined with increasing ω, while strong positive persistence also reduced occupancy when the probability of cue-driven bias was low. At β_{max} = 0.5, low occupancy occurred across a broad range of parameter combinations, particularly at high ω or strongly positive α. These patterns indicate that persistence and cue-following can each promote movement out of the cash crop, but their relative importance depends on attraction strength. Increasing β_{max} reduced sensitivity to the precise value of α over much of the parameter space, because frequent responses to the attraction cue produced consistently low cash crop occupancy.

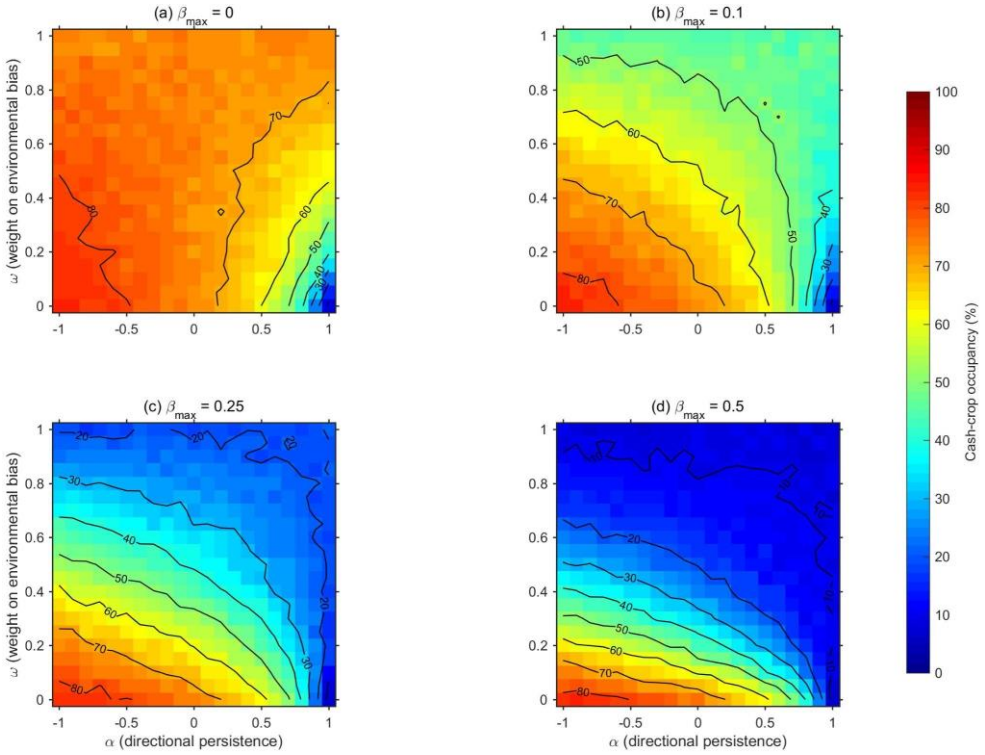

Figure 5. Cash-crop occupancy across directional persistence (α) and environmental-bias weight (ω) for different maximum attraction strengths (β_{max}). Each heatmap shows the percentage of the initial insect population remaining in the cash crop at t = 15 days for all combinations of $\alpha \in [-1, 1]$ and $\omega \in [0, 1]$, with β_{max} = 0, 0.1, 0.25, or 0.5. Warmer colours indicate higher cash-crop occupancy, and labelled contour lines indicate equal occupancy percentages. All other parameters are as in Fig. 2.

3.2 Insect removal and arrestment dynamics

Variation in entry interception, within-trap crop removal, and arrestment alters the temporal redistribution of insects among the four population states tracked by the model. Across all scenarios, the proportion of insects remaining in the cash crop generally declines through time as individuals enter the trap crop or emigrate beyond either field boundary (Fig. 6a). Differences among scenarios remain relatively small during the early phase of the simulation but become more pronounced over longer time scales. This occurs because the parameters varied in this section (γ_{entry}, γ_{day} and ρ) act primarily after insects reach the trap crop and do not directly determine the rate at which insects initially leave the cash crop. Instead, the rate at which insects encounter the trap crop boundary is determined by the movement parameters governing attraction and behaviour within the cash crop (β, ω, and α), which influence how frequently insects respond to trap crop-associated cues and how strongly they maintain directional persistence. However, interception, mortality, and arrestment subsequently affect cash crop occupancy by determining whether individuals are removed, retained within the

trap crop, or able to return to the cash crop. Consequently, the simulations in Fig. 6 primarily isolate how different interception and retention mechanisms influence the removal outcome once the trap crop strip has been encountered rather than how rapidly insects initially depart the cash crop. By the end of the simulation, the lowest cash crop occupancy occurs when within-trap crop removal is absent, followed closely by the no-arrestment scenario, whereas baseline conditions, no entry interception, and perfect entry interception retain comparatively higher cash-crop occupancy.

In contrast, the mechanisms governing interception, removal, and retention generate pronounced differences in the dynamics within the trap crop and in the resulting fates of intercepted individuals. Under baseline conditions, trap crop occupancy initially increases as insects accumulate within the trap crop strip before gradually declining as individuals are removed or emigrate (Fig. 6b). Eliminating within-trap crop mortality leads to higher trap crop occupancy during the early phase of the simulation followed by a gradual decline as insects leave the field, while strong arrestment combined with weak within-trap crop removal produces a sustained increase in trap crop occupancy throughout the simulation. When arrestment is absent, trap crop occupancy remains low because individuals traverse the trap crop strip rapidly, whereas perfect entry interception results in essentially zero trap crop occupancy because insects are removed immediately upon crossing the cash crop–trap crop boundary. These differences are reflected in the cumulative removal and current emigration dynamics (Fig. 6c–d). Removal increases steadily through time in all scenarios but reaches substantially higher levels when entry interception is perfect, while scenarios lacking within-trap crop mortality accumulate removal more slowly. Emigration exhibits a broadly opposing pattern. The largest proportions currently outside the field occur when within-trap crop removal is absent and when arrestment is absent, because more individuals survive passage through the trap crop and cross the field boundary. Strong arrestment with weak lethality reduces emigration relative to these scenarios but does not eliminate it, whereas perfect entry interception results in negligible emigration because individuals are removed upon entering the trap crop.

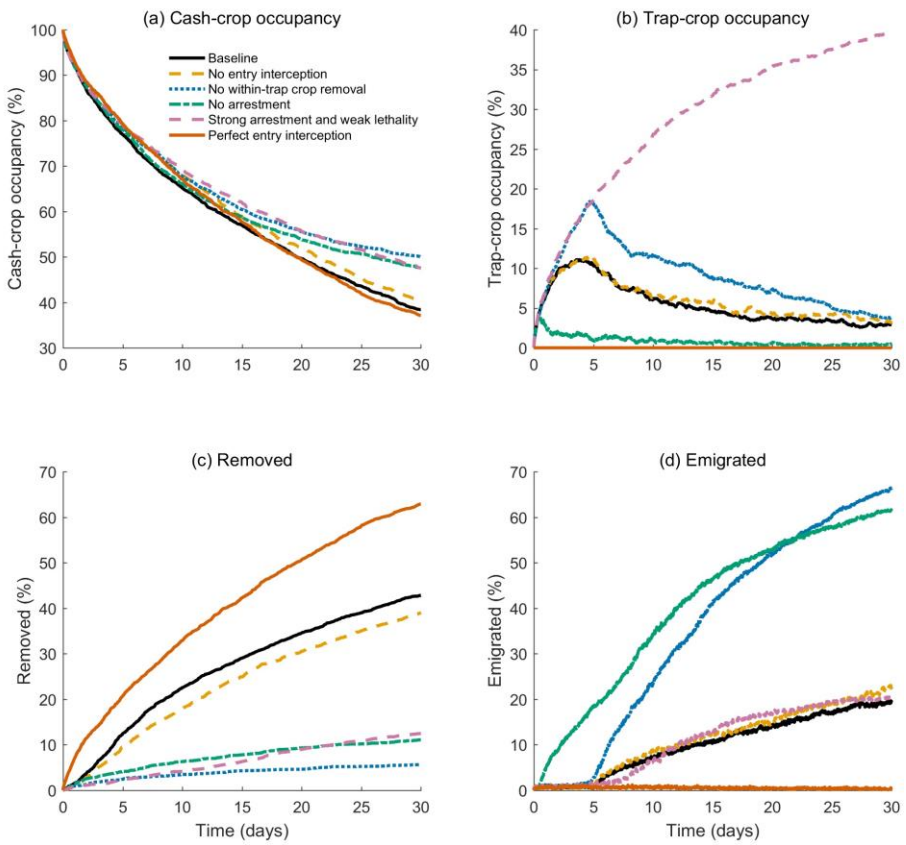

Figure 6. Effects of trap crop interception, within-trap crop removal, and arrestment on trap cropping dynamics. Time-series simulations from the model described in Fig. 1 show the temporal evolution of the four population states over 30 days: (a) the proportion of individuals remaining in the cash crop, (b) the proportion located within the trap crop, (c) the cumulative proportion removed, and (d) the proportion currently emigrated beyond either field boundary. All quantities are expressed as percentages of the initial population $N_0 = 2500$ and together sum to 100% at each time point. Individuals are initially distributed uniformly within the cash crop, as in Fig. 2. Six scenarios are shown to isolate the roles of the main trap crop mechanisms: baseline dynamics, using the same parameterisation as Fig. 2; no entry interception ($\gamma_{entry} = 0$); no within-trap crop removal ($\gamma_{day} = 0$); no arrestment ($\rho = 1$); strong arrestment with weak within-trap crop lethality ($\rho = 0.01$, $\gamma_{day} = 0.01$); and perfect entry interception ($\gamma_{entry} = 1$), representing an idealised dead-end trap crop.

Figure 7 examines how trap crop width influences the redistribution of insects among the four population states when evaluated at a fixed time point ($t = 15$ days). Across all scenarios, increasing the cash crop fraction k (i.e., reducing the width of the trap crop) results in higher proportions of insects remaining within the cash crop (Fig. 7a). This pattern reflects the increasing width of the cash crop and the reduced width of the trap crop, which reduce exposure of individuals to the trap crop region during movement. Differences among the scenarios remain comparatively small for cash crop occupancy, consistent with the behaviour observed in Fig. 6. Because the parameters varied here (γ_{entry}, γ_{day}, and ρ) act upon entry to or within the trap crop, they primarily influence the fate of intercepted individuals rather than

the initial rate at which insects depart the cash crop. Consequently, the curves in Fig. 7a remain relatively close across scenarios, with strong arrestment and weak lethality generally producing the lowest values.

In contrast, trap crop occupancy is strongly affected by both trap crop width and the interception and retention mechanisms operating within the trap crop strip. Wider trap crop areas (smaller k) allow greater accumulation of insects within the trap region, particularly when arrestment is strong and within-trap removal is weak (Fig. 7b). Under this scenario, insects remain within the trap crop strip for extended periods, but occupancy declines as the trap crop strip narrows. When arrestment is absent, insects move rapidly through the trap crop strip and trap crop occupancy remains low regardless of trap crop width. Perfect entry interception results in near-zero trap crop occupancy because insects are removed upon entry to the trap crop. These patterns illustrate that trap crop width interacts strongly with behavioural retention: wider trap crops amplify the effects of arrestment by increasing the distance over which reduced movement operates within the trap crop strip.

The resulting differences in removal and emigration outcomes are reflected in Fig. 7c–d. Removal is generally highest when trap crop width is widest and entry interception strongest, with the perfect entry-interception scenario producing the greatest cumulative removal across all trap crop widths. Under baseline conditions, removal declines gradually as the trap crop strip narrows due to the reduced opportunity for insects to encounter and remain within the trap crop. Scenarios lacking within-trap crop mortality produce lower cumulative removal, while strong arrestment with weak killing produces comparatively low overall removal despite high trap occupancy. Emigration varies more strongly among scenarios; the absence of arrestment generally generates among the highest levels of emigration, whereas perfect entry interception produces the lowest emigration, while strong arrestment with weak lethality produces intermediate levels. These results demonstrate that cash–trap crop allocation primarily controls the likelihood of trap crop encounter, while the retention and removal mechanisms determine the ultimate fate of insects once the trap crop has been reached.

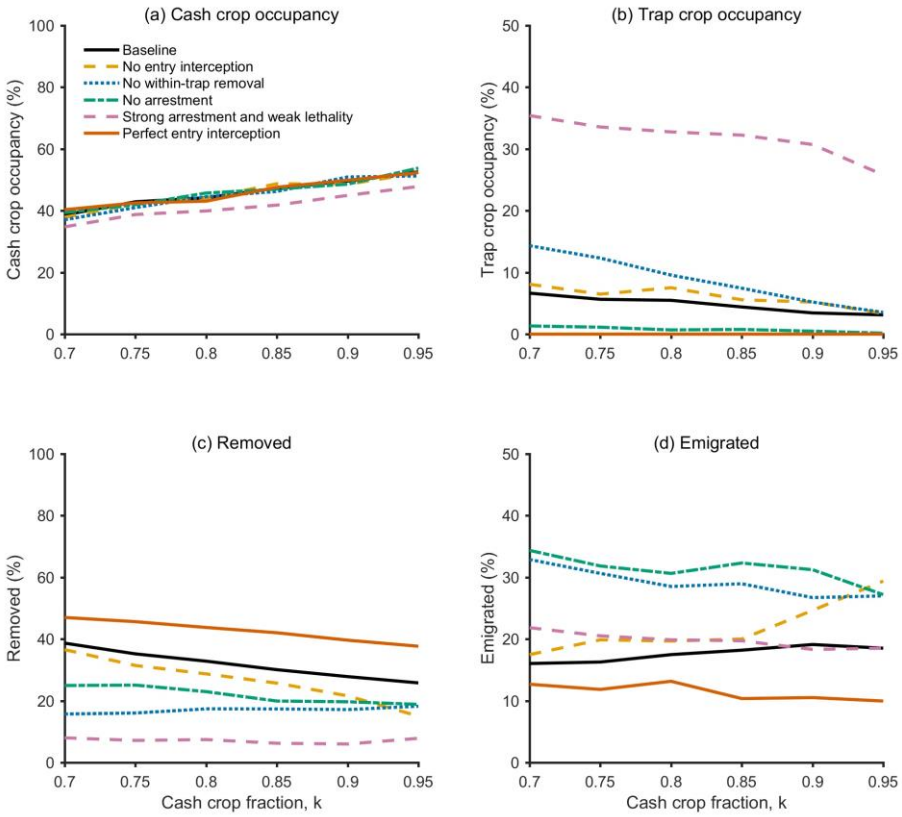

Figure 7. Influence of trap-crop width on pest redistribution under different interception, removal, and arrestment scenarios. Simulations from the model described in Fig. 2 show the distribution of individuals across four population states at $t = 15$ days as a function of the cash crop fraction k, with individuals initially distributed uniformly within the cash crop. Panels show: (a) cash crop occupancy, (b) trap crop occupancy, (c) cumulative removal, and (d) emigration beyond either field boundary. The horizontal axis varies from $k = 0.70$ to 0.95, corresponding to trap crop coverage of 30 to 5% of the field. Curves represent six scenarios: baseline; no entry interception ($\gamma_{entry} = 0$); no within-trap removal ($\gamma_{day} = 0$); no arrestment ($\rho = 1$); strong arrestment with weak lethality ($\rho = 0.01$, $\gamma_{day} = 0.01$); and perfect entry interception ($\gamma_{entry} = 1$), representing an idealised dead-end trap crop.

Increasing γ_{entry} produces a relatively direct rise in removal because individuals are eliminated immediately as they enter the trap crop (Fig. 8). This may, for example, reflect the effect of a contact pesticide or another interception-based control measure. In contrast, increasing γ_{day} produces removal during residence within the trap crop and could represent mortality arising from prolonged pesticide exposure, ingestion of toxic plant tissue, or exposure to biological control agents. The influence of within-trap removal is stronger when movement is reduced within the trap crop ($\rho = 0.1$), because longer residence increases cumulative exposure.

Behavioural arrestment also substantially reduces emigration, particularly when within-trap removal is present. Without arrestment ($\rho = 1$), insects move through the trap crop more rapidly, making entry-triggered removal relatively more important and producing

greater emigration when both removal probabilities are low. These patterns show that entry-triggered and within-trap removal operate through different exposure regimes, with behavioural arrestment modulating their relative importance by altering insect residence time within the trap crop.

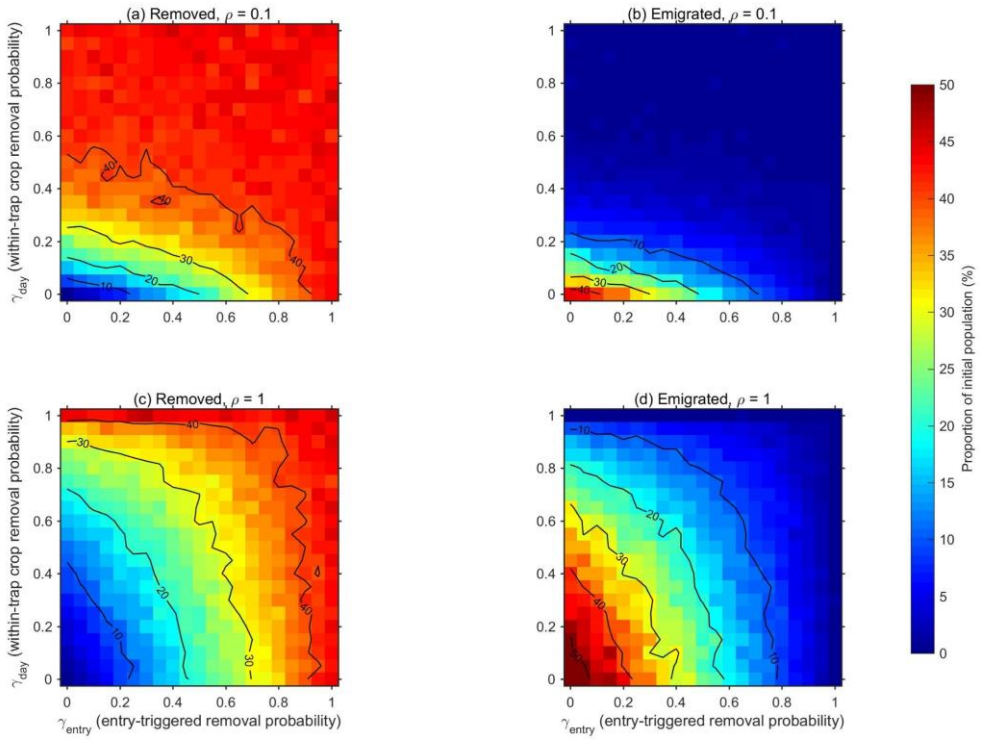

Figure 8. Combined effects of entry-triggered removal, within-trap removal, and behavioural arrestment on pest population outcomes. Heatmaps show the proportion of the initial population removed (left column) and located beyond either field boundary (right column) after 15 days, across combinations of entry-triggered removal probability (γ_{entry}) and daily within-trap removal probability (γ_{day}). The top row shows simulations with behavioural arrestment in the trap crop ($\rho = 0.1$), whereas the bottom row shows simulations without arrestment ($\rho = 1$). The parameter ρ scales movement step length within the trap crop and therefore influences residence time. Entry-triggered removal occurs when insects cross from the cash crop into the trap crop, while within-trap removal acts on insects remaining in the trap crop. Individuals are initially distributed uniformly within the cash crop, and all values are expressed as percentages of the initial population.

4. Discussion

4.1 A movement-based extension of trap crop modelling

Existing modelling approaches to trap cropping have made important contributions by isolating specific mechanisms, but they typically emphasise different components of the system rather than treating them within a unified framework. Models in heterogeneous crop systems have focused on pest movement and spatial processes, often representing dispersal

using diffusion-based formulations derived from random walk processes (Perry and Wall, 1984; Hannunen, 2005), including extensions with predator-prey dynamics to model biological control (Banks and Laubmeier, 2024), as well as individual-based and spatially explicit movement models (Vinatier et al., 2012; Garcia et al., 2021). These approaches capture large-scale redistribution effectively, but do not jointly represent directional responses to host-plant cues, movement persistence, and post-arrival retention. Complementing these approaches, discrete patch- and lattice-based formulations that represent the system at the level of individual plants or patches, have been used to incorporate attraction, retention, and plant configuration through local transition rules (Banks and Ekbom, 1999; Holden et al., 2012). Under a set of non-conflicting assumptions these models are often analytically tractable and have been particularly important in demonstrating that trap crop performance depends on the balance between attraction towards and dispersal away from the trap crop (Holden, 2026a, 2026b).

Our approach provides a unified, flexible framework that integrates pest movement behaviour, attraction, and retention. Like previous approaches, it captures insect attraction to and retention within the trap crop, but does so by explicitly representing directional movement through the landscape, rather than relying solely on diffusion or patch-transition probabilities. This is particularly relevant in systems where orientation towards plant-associated cues influence interception dynamics, which purely diffusion formulations cannot represent directly. As a result, the framework offers greater mechanistic resolution for identifying the conditions under which trap crops are effective, while remaining sufficiently structured to yield general insights comparable to existing analytical and spatial models.

A key distinction of our model is the inclusion of directional persistence in pest movement, the tendency of individuals to continue moving in their current direction. This differs from previous models, which implicitly assume that movement is memoryless, i.e., insects diffuse randomly regardless of their previous direction. By incorporating persistence through a biased correlated random walk, our framework is able to capture more detailed and potentially more realistic movement patterns, consistent with empirical and theoretical studies of insect and arthropod movement (Kareiva and Shigesada, 1983; Byers, 2001; Petrovskii et al., 2014; Ahmed et al., 2023). Our framework therefore allows the role of directional persistence, and its interaction with attraction, to be examined explicitly in trap-cropping systems.

In our model, persistence altered pest distributions in the cash and trap crops compared to cases where insects moved in a biased, but uncorrelated (memoryless) fashion. Increasing positive persistence (i.e., the probability of continued movement in the current direction) consistently decreased the proportion of pests on the cash crop. Furthermore, it interacted with bias (attraction), with the lowest cash-crop occupancy generally occurring when both attraction and persistence were high. While empirical studies in the trap cropping literature are dominated by efforts to measure and optimise the attractiveness of potential trap crop plants (Holden et al., 2012; Holden, 2026b), persistence of insect movement in trap cropping systems, as far as we are aware, remains entirely unexplored. If movement persistence varies among pest species or is modified indirectly by local habitat structure, such as vegetation density, crop row orientation, or physical resistance to movement, it may represent an additional mechanism influencing trap crop performance. Determining when persistence is intrinsic, environmentally mediated, or experimentally manipulable, may present a novel avenue for improving trap cropping design.

4.2 Ecological implications for trap crop performance

By explicitly incorporating directional bias in movement, our framework provides a more realistic representation of how pests respond to biologically meaningful cues, creating a closer link between plant traits, pest sensory ecology, and spatial dynamics in the field. This is important because insect movement responses are expected to vary among species according to their life history, including host preferences, foraging state, mobility, and physiological state (Minkenberg et al., 1992; Hochuli, 2001; Scheirs and De Bruyn, 2002; Shelton and Badenes-Pérez, 2006; Badenes-Pérez et al., 2006). For example, adult Colorado potato beetles (*Leptinotarsa decemlineata*) represent a well-studied example of a pest in which local movement, host-associated cues, feeding state, and landscape structure influence spatial redistribution (Landolt et al., 1999; Boiteau et al., 2003; Gui et al., 2012). Trap crops can intercept and concentrate dispersing beetles within a restricted area, allowing targeted removal through well-timed, selective insecticide application (Hunt and Whitfield, 1996; Martel et al., 2005). Their effectiveness nevertheless depends on whether species-specific responses to the trap crop promote movement towards it and provide sufficient retention for removal mechanisms to act.

However, the effectiveness of attraction-based strategies also depends on the relative attractiveness of the trap crop compared with the cash crop. In Colorado potato beetle

management, trap crop effectiveness depends on the relative attractiveness of the trap and cash crops. For example, potato (*Solanum tuberosum*) trap crops can divert pest pressure away from tomato (*Solanum lycopersicum*) crops, reducing beetle abundance on the protected crop (Hunt and Whitfield, 1996). However, when potato itself is the cash crop, the effectiveness of trap crops may be limited unless additional measures are implemented to retain or remove beetles within the trap crop (Hoy et al., 2000). For example, *Bacillus thuringiensis* (Bt) transgenic potatoes planted earlier than the potato cash crop have been suggested as a dead-end trap crop for Colorado potato beetle, although so far they have not been tested as such (Shelton and Badenes-Pérez, 2006; Badenes-Pérez, 2025). Enhancing attraction through additional cues, such as synthetic aggregation pheromones, may represent another approach for increasing interception when trap crops are not sufficiently attractive relative to the cash crop (Kuhar et al., 2006).

Our results show that attraction was most effective when cues extended across a broad portion of the cash crop, suggesting that trap crop strategies are more likely to succeed when pests can detect and orient toward their hosts from a distance. Similar trap cropping designs therefore cannot be expected to perform consistently across systems, because different species vary in their behavioural responses to plant cues and because abiotic and biotic conditions can alter cue production, transmission, detection, and the resulting movement response (Shelton and Badenes-Pérez, 2006). For example, crop borders and host-plant connectivity can alter local movement paths and retention of adult Colorado potato beetles, with non-host vegetation acting as a barrier to movement between potato patches (Boiteau et al., 2014). Although such spatial complexity is simplified in our one-dimensional framework, these findings illustrate how local crop structure can modify encounter and retention processes and thereby influence trap crop performance.

Even when attraction is strong enough to draw pests away from the cash crop, trap crop effectiveness ultimately relies on whether movement within the trap crop is sufficiently reduced to prolong residence and allow removal mechanisms to act. More broadly, the relative allocation of the field to cash and trap crops influenced pest encounter, but trap crop effectiveness depended strongly on post-encounter behaviour, suggesting that spatial design and behavioural retention must be considered together. Immediate removal may arise from strategies such as contact insecticides, sticky surfaces, or other interception-based measures, whereas delayed removal may depend on residence time within the trap crop and be mediated by insecticide application, plant toxins, and/or predation (Badenes-Pérez, 2025). If retention

is weak, however, even a highly attractive trap crop may fail to manage the insect pest (Holden et al., 2012).

By separating encounter, retention, and removal into distinct processes, our framework helps explain why a trap crop may succeed or fail. Failure may be due not to low attractiveness, but to pests not remaining in the trap crop or not being removed efficiently. This distinction has practical implications for management strategies since some systems may benefit from trap crops designed primarily to intercept and retain insects, whereas others may require targeted suppression through insecticide application, addition of natural enemies, or other control measures within the trap crop itself. By making these mechanisms explicit, simulation models such as ours offer a useful tool for understanding why trap cropping succeeds or fails under particular ecological conditions, thereby guiding more informed decisions about trap crop width, land allocation, and complementary management strategies.

4.3 Advancing predictive trap crop modelling

Future work should build on our modelling approach by extending both its spatial and ecological scope while retaining analytical clarity. A first priority is the incorporation of more realistic spatial structure. Although equilibrium pest distributions under random walk assumptions may be insensitive to configuration, the transient dynamics that determine practical pest suppression depend strongly on patch geometry, including patch size, shape, and perimeter-to-area ratios (Hannunen, 2005; Perry and Wall, 1984). In particular, the placement and spatial arrangement of trap crops within two-dimensional landscapes, including their position relative to field boundaries, their spatial distribution (e.g. strips, borders, or dispersed patches), and their size, are expected to play a critical role in determining interception efficiency and retention. Embedding these geometric features within the present movement–attraction–retention framework would allow the analysis of how spatial layout influences not only redistribution but also the timescale over which trap crops become effective. This is particularly relevant for short cropping cycles or systems subject to continuous pest migration, where transient dynamics rather than equilibrium states determine outcomes.

Another aspect concerns the potential role of demographic processes, in particular mate-searching behaviour and population growth. In temperate regions, where life cycles tend to be more synchronised and the foraging period may not overlap substantially with reproductive activity, these processes are likely to have a limited influence on the dynamics

captured by the model. By contrast, in tropical environments, where smaller seasonal temperature fluctuations can lead to more continuous or desynchronised population dynamics, demographic processes may become more relevant and could meaningfully modify model predictions (e.g. Godfray and Hassell, 1987; Vinatier et al., 2009). In such contexts, the interaction between movement, reproduction, and mortality may need to be explicitly considered in order to fully capture pest dynamics.

As part of the agroecological transition, numerous practices are emerging, leading to increased diversification of agricultural landscapes (e.g., agroforestry, enhanced field margin complexity, and species mixtures) (Molénat et al., 2023). These systems can, in principle, be represented within our modelling framework; however, they require additional conceptual work to translate the emerging spatial configurations associated with these practices into a one-dimensional representation. In particular, careful abstraction is needed to ensure that key structural and functional properties of these more complex spatial patterns are preserved within the simplified modelling domain.

Alongside these theoretical developments, empirical validation is required to test the mechanistic predictions of the model. In particular, controlled field and semi-field experiments that quantify pest movement, attraction, and retention across alternative trap crop configurations would allow direct evaluation of the processes represented in the model. Previous work has demonstrated the dominant role of retention relative to attraction in determining trap crop efficacy (Holden et al., 2012), but systematic measurements that separate these mechanisms remain limited. The modelling approach developed here provides a basis for designing such experiments, as its parameters correspond directly to measurable quantities, allowing hypotheses on directional movement, interception, and retention to be tested explicitly under field conditions. Integrating experimental observations with the model would enable parameter estimation, calibration, and validation across crop–pest systems, thereby strengthening the predictive capacity of the approach.

Another important direction concerns the representation of movement behaviour. While the current formulation incorporates directional bias towards trap crops, it assumes a relatively simple structure for movement. In practice, insect movement may involve switching between behaviours, persistence in direction, or non-diffusive dispersal patterns. Extending the model to include such mechanisms would strengthen the connection between individual-level behaviour and population-level redistribution, and would allow comparison with both diffusion-based limits and individual-based formulations. In addition, linking

model parameters to measurable quantities such as motility, residence time, and turning behaviour would improve empirical interpretability and facilitate calibration. It is now possible to estimate these parameters thanks to the rise of insect tagging and tracking techniques (e.g., El Sheikha, 2019; Hüppop et al., 2019) and their appropriate analyses (Rüppel et al., 2026). A third extension is the inclusion of additional ecological processes. The present framework focuses on movement-driven redistribution, but trap cropping outcomes are also influenced by population dynamics, including reproduction, mortality, and interactions with natural enemies. Incorporating predator–prey or parasitoid dynamics, inter- and intraspecific competition, as well as temporal variation in plant attractiveness to different insect life stages, would enable the model to capture seasonal effects and stage-specific vulnerabilities. Such extensions would also allow investigation of how trap crops function as both sinks and potential sources of pests under different ecological conditions.

Finally, there is a need to integrate our mechanistic modelling with optimisation and decision-making approaches. Optimal allocation of land to trap crops depends on trade-offs between pest suppression and yield loss, often requiring a non-negligible proportion of the landscape to be devoted to trap crop plants (Shelton and Badenes-Pérez, 2006; Holden, 2026b). Embedding these economic and agronomic considerations within the present framework would enable the derivation of design principles that jointly account for movement dynamics, spatial structure, and yield outcomes. More broadly, future research should aim to identify general thresholds in key parameters such as retention, attraction, and pest mobility that determine transitions between ineffective and effective trap cropping. Establishing such criteria would contribute to a more predictive and general theory of trap cropping systems.

5. Concluding remarks

We developed a movement-based trap cropping framework that explicitly integrates attraction, directional persistence, behavioural arrestment, and pest removal within a single mechanistic model. Our results show that trap crop effectiveness depends on the interaction of these processes rather than on attraction alone. Attraction acting across a broad portion of the cash crop increased encounters with the trap crop, while directional persistence and attraction acted synergistically to reduce pest occupancy within the cash crop. However, successful encounters did not necessarily translate into effective suppression, as strong attraction alone was often insufficient when insects were not retained following arrival.

822 Instead, behavioural arrestment emerged as a key determinant of post-encounter outcomes,
823 while entry-triggered removal and within-trap crop removal operated through distinct
824 mechanisms. We further found that wider trap crop strips increased opportunities for
825 encounter, while strengthening the effects of retention and removal, highlighting important
826 interactions between behavioural processes and spatial design. More broadly, these findings
827 help explain why trap cropping systems can produce highly variable outcomes in practice
828 (Hokkanen, 1991; Shelton and Badenes-Pérez, 2006; Cook et al., 2007). Effective trap crops
829 must not only attract pests, but also retain them long enough for suppression mechanisms to
830 act (Holden et al., 2012; Badenes-Pérez, 2025). By explicitly separating the processes of
831 encounter, retention, and removal, the framework provides a mechanistic basis for
832 understanding trap crop performance across a range of trap-cropping scenarios and offers a
833 foundation for incorporating behavioural ecology more directly into the design and
834 evaluation of ecologically based pest-management strategies.

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CRediT authorship contribution statement

Danish A. Ahmed: Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing – original draft, Writing – review and editing. **Noor Tahat:** Conceptualization, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – review and editing. **Joseph D Bailey:** Methodology, Visualization, Writing - original draft, Writing - review and editing. **Isadora E. Fluck:** Writing – original draft, Writing – review and editing. **Matthew H. Holden:** Writing – original draft, Writing – review and editing. **Francisco Rubén Badenes-Pérez:** Writing – original draft, Writing – review and editing. **Emma J. Hudgins:** Writing – review and editing. **Philip E. Hulme:** Writing – review and editing. **Fabrice Vinatier:** Writing – review and editing.

Declaration of competing interest

The authors declare that they have no competing financial interests or personal relationships that could have influenced the work reported in this paper.

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Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During preparation of this manuscript, the authors used ChatGPT to assist with language editing and improve readability. The authors reviewed and edited all content and take full responsibility for the final manuscript.

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